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Butterfly Optics Exceed the Theoretical Limits of Conventional Apposition Eyes

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Abstract. Optical experiments on butterfly compound eyes show that they have angular sensitivities narrower than expected from conventional apposition eyes. This superior performance is explained by a theoretical model where the cone stalk is considered as a modecoupling device. In this model the Airy diffraction pattern of the corneal facet excites a combination of the two waveguide modes LP_{01} and LP_{02}. When the two modes propagate through the cone stalk the power of LP_{02} is transferred to LP_{01} alone which is supported by the rhabdom. This mechanism produces a higher on-axis sensitivity and a narrower angular sensitivity than conventional apposition optics. Several predictions of the model were confirmed experimentally.

1 Introduction

The accepted model of optics in apposition compound eyes is simple, consisting of a waveguide photoreceptor in the focal plane of a lens (Snyder 1975, 1977; Pask and Barrell 1980a, b; Van Hateren 1984). A major exception from this model was recently found in butterfly apposition eyes by Nilsson et al. (1984, 1987). With several optical techniques they demonstrated that the butterfly optical system behaves as an afocal telescope. The principal difference from conventional apposition optics is the addition of a small but powerful lens in the cone stalk. This second lens recollimates the light from a point source so that it reaches the rhabdom as a parallel bundle. This is indeed a new concept in apposition eye optics, but the existence of such an optical system still lacks a functional explanation. In a theoretical study by Dr. Colin Pask (pers. comm.) the afocal system is shown to perform no better than a conventional apposition system with focal optics, at least if the cone-stalk lens is considered as an ideal lens. It is intriguing, therefore, that butterflies have evolved such a substantial elaboration of their ommatidial optics with seemingly no improvement.

The main intention of this article is to provide a theoretical interpretation of butterfly optics that allows a functional explanation. As will be shown in this paper, the system is indeed superior to conventional apposition systems in two respects. First, it yields a higher on-axis sensitivity, second, it brings the angular sensitivity closer to the diffraction limit of the facet lens. We first provide experimental data on the performance of butterfly optics, and compare it with the conventional apposition system of the fly (see Van Hateren 1984). Although the afocal model of butterfly optics seems inevitable from the observations reported by Nilsson et al. (1987), we have here adopted quite a different interpretation. From the micrometer dimensions of the cone-stalk lens it is clear that it must act as a waveguide to some degree. If the entire cone stalk is considered part of the waveguide, the ommatidial optics can be modelled as a focal system with a funnel-shaped inhomogeneous distal end of the waveguide. In this paper we will show that predictions from such a model agree very well with experimental data, and also that the model provides important clues to the evolution of the butterfly optical system.

2 Methods

2.1 Animals and Preparation

Quantitative measurements were performed on the Sulfur butterfly, *Gonepteryx rhamni*. Results were obtained from seven ommatidia in two butterflies. The results were similar for all ommatidia. Additional qualitative observations were made on the following butterflies: *Clossiana euphrosyne*, *Aphantopus hyperantus*, and *Lycaena phlaeas*. The anatomy was inves-

tigated in all the above species and also in *Argynnis paphia*. For all optical experiments unanaesthetized animals were fixed with wax, and mounted on an $x-y-z$ stage. Care was taken not to impair ventilation.

2.2 Optical Methods and Rationale

The optical instrument used for the experiment of Fig. 1 is an extension of the one described previously (Van Hateren 1984). The main extension was a small halfmirror mounted in front of the objective, used for applying orthodromic light. This light travels through the ommatidia first in the orthodromic direction, is reflected by the tapeta, and propagated back in the antidromic direction. The light radiating out of the eye is then collected by the objective of the instrument, spatially filtered to select radiation coming from a single ommatidium, and finally imaged in the far field (see Franceschini 1975; Van Hateren 1984; Nilsson et al. 1987). The image is recorded photographically and then analyzed with a microdensitometer, which yields the intensity distribution of the far field radiation pattern of the eye.

As shown in Van Hateren (1984) this far field radiation pattern is – at least in lens-waveguide systems – identical to the angular sensitivity. Although we will argue in this article that the butterfly has a system more complex than just a lens-waveguide system, the far field radiation pattern is identical to the angular sensitivity also in this system. The reason for this is that the Helmholtz reciprocity theorem used in the argument in Van Hateren (1984) is also valid for the optical system we propose here for the butterfly. The reciprocity theorem, however, is only applicable to one mode at a time because, if e.g. two modes are present, the one that is most efficiently absorbed by the photopigment will contribute least to the light that is returned from the eye and is used for the optical measurements (Van Hateren 1984; Nilsson et al. 1987). To avoid this problem we have, for the optical experiments, selected butterfly species that only support the first mode (LP_{01}) in their rhabdoms (see Land et al. 1987).

Further details on the optical setup, the photography, and the calibration are given in Van Hateren (1984). The photographs of radiation patterns (Figs. 4 and 6) were made on another optical setup which is based on the same general principle as the one mentioned above. More details on this setup and the various ways of imaging the output of butterfly eyes are given in Nilsson et al. (1987).

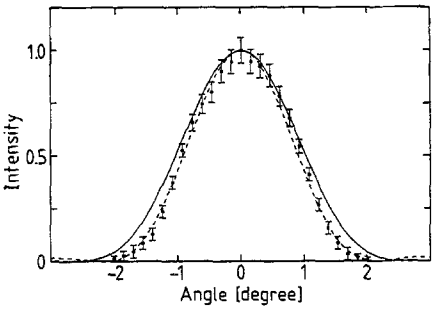

Fig. 1. Angular sensitivity of the Sulfur butterfly. *Data points:* intensity of the far-field radiation pattern of an ommatidium produced by reflection of orthodromic light at the tapetum; wavelength 650 nm, lens diameter 21 μm (inscribed circle 20 μm, circumscribed circle 22 μm). Broken line: Airy diffraction pattern for a 21 μm lens. Continuous line: angular sensitivity for a lens-fiber system with the same lens diameter and an F-number that yields an optimum on-axis efficiency ($F=2.2$, rhabdom diameter 2 μm)

2.3 Anatomy

For electron microscopy, shallow eye cups were cut from fresh eyes. The cups were fixed in a solution consisting of 2% formaldehyde, 2.5% glutaraldehyde, 4% sucrose and 10 m*M* EGTA in 0.2 *M* sodium cacodylate buffer (pH 7.3). Postfixation was carried out in 1% OsO_4 solution. The material was dehydrated in an alcohol series and embedded in Araldite. Ultrathin sections were cut and stained with lead citrate and uranyle acetate.

3 Results

3.1 Measurements of the Angular Acceptance Function

Figure 1 shows the acceptance function measured (see Methods) in the Sulfur butterfly (data points), and two theoretical angular sensitivities. The dimensions of the ommatidial lens were also determined. For the theoretical calculations we assumed a circular lens with a diameter equal to the mean of the inscribed and circumscribed circles of the hexagonal lens. This diameter yielded the Airy diffraction limit of the lens (broken line). The second theoretical curve (continuous line) is the one that corresponds to a conventional apposition eye: a facet lens with a waveguide in its focal plane (as is found e.g. in the fly's eye, see Van Hateren 1984; Smakman et al. 1984). The F-number of the lens was optimized here for maximum on-axis efficiency (about 80%).

We see in Fig. 1 that the measured points are closer to the Airy diffraction limit than to the curve corresponding to a pure lens-waveguide system. This was the case in all ommatidia where this measurement was done. The optics of butterfly ommatidia appear to produce angular sensitivities narrower than expected

from a conventional apposition system. We propose in this article that this may be caused by a better match to the Airy diffraction pattern realized through mode-coupling in the cone stalk of the butterfly ommatidium.

3.2 *Mode-Coupling of LP_{01} and LP_{02} as a Hypothesis*

In general an eye faces the task of collecting light efficiently and using it for obtaining an image of its surroundings (Snyder et al. 1977). Often this is accomplished by the combination of a lens and one or more waveguides. The lens concentrates the light on the entrance of the waveguide, where it is trapped in so-called bound modes, which propagate along the waveguide (Horowitz 1981). This system is quite efficient: about 80% of the light falling on-axis on the lens is trapped in the waveguide. Also the directional properties are good: lens and waveguide together produce an angular sensitivity close to the diffraction limit of the lens (the theoretical minimum for an ideal lens of a given diameter and for a given wavelength of the light). The angular sensitivity will in practice be somewhat broader than the Airy diffraction limit because of the aperture of the waveguide, but only about 15–20% in a well-designed lens-waveguide system like that of the fly (Van Hateren 1984).

Both figures mentioned above, the 80% on-axis efficiency, and the 15% broadening of the Airy diffraction limit, depend on how well the Airy diffraction pattern, projected by the lens onto the waveguide aperture, is matched by the modes that can propagate in the waveguide. In fact, if a mode that mimicked the Airy pattern perfectly existed, the on-axis efficiency would be 100%, and the broadening of the Airy pattern 0% (Van Hateren 1984; Nilsson et al. 1987). Figure 1 suggests that the butterfly ommatidium behaves better than expected from the conventional lens-waveguide system, and we propose that this is accomplished by a specialization of the cone stalk (see below) that supports an electromagnetic pattern mimicking the Airy diffraction pattern better than the LP_{01} mode which has that role in the fly's eye.

Our hypothesis is that the Airy pattern excites a mixture of the modes LP_{01} and LP_{02}, which become coupled (Snyder 1970; Snyder and Love 1983) when they propagate through the cone stalk. These modes can become coupled in the cone stalk, because they have the same angular symmetry (being both circularly symmetrical), and because the cone stalk is tapered and has an inhomogeneous refractive index (see below). This coupling is assumed to be such, that all the power of LP_{02} is transferred to LP_{01} before the light arrives at the rhabdom entrance. The consequences of this are illustrated in Fig. 2. In Fig. 2A the modes LP_{01} and LP_{02} are shown as they are excited by an Airy

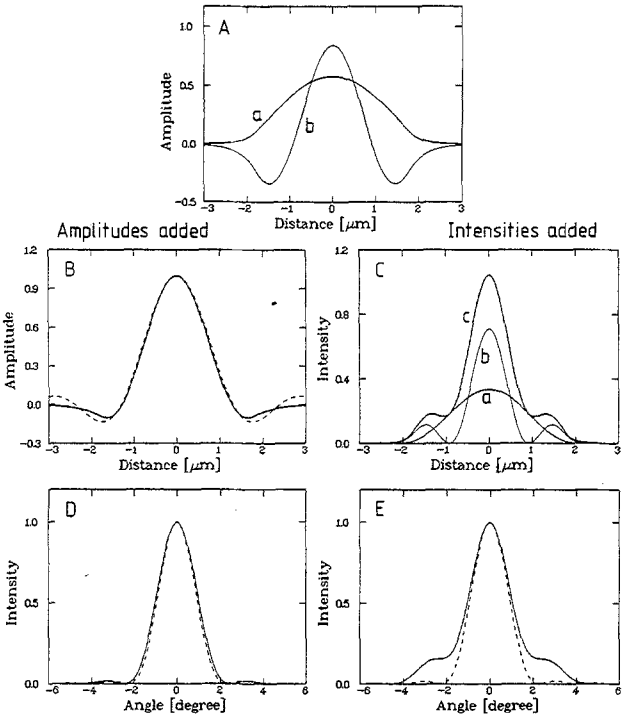

Fig. 2A–E. The modes LP_{01} and LP_{02} may produce angular sensitivities close to the diffraction limit if their amplitudes are added. **A.** Modes LP_{01} (*a*) and LP_{02} (*b*) at the cone stalk. Parameters: cone stalk diameter 3.6 μm, refractive index of the cone stalk 1.4, refractive index of surrounding media 1.35, wavelength 650 nm. **B.** An Airy diffraction pattern *(broken line)* excites LP_{01} and LP_{02} such that their amplitude superposition *(continuous line)* closely matches the Airy pattern. Parameters as in *A*, lens diameter 20 μm, *F*-number 1.65. **C.** The intensity superposition (*c*) of LP_{01} (*a*) and LP_{02} (*b*) matches the Airy pattern less well. **D.** The far field radiation pattern of the ommatidium formed by amplitude superposition of LP_{01} and LP_{02} *(continuous line)* and the Airy pattern *(broken line)*. **E.** The far field radiation pattern following from intensity superposition of LP_{01} and LP_{02} *(continuous line)* and the Airy pattern *(broken line)*

diffraction pattern projected by the lens onto the distal end of the cone stalk. If the amplitudes of these modes are added (Fig. 2B, continuous line) we get a pattern very close to the original Airy pattern (Fig. 2B, broken line), much closer than LP_{01} alone would yield. The main lobe of the Airy pattern and the first fringe are quite well matched; higher fringes, however, are not matched at all. The resulting angular sensitivity, shown in Fig. 2D (continuous line), is quite close to the Airy diffraction limit of the lens (Fig. 2D, broken line).

In Fig. 2B and D the *amplitudes* of LP_{01} and LP_{02} are added. This is only justified because we assume that they are coupled such that all the power of LP_{02} is transferred to LP_{01} before being absorbed in the rhabdom. This should not be confused with the case where the rhabdom is so wide that it can propagate

LP_{01} as well as LP_{02}, in which case we must add their *intensities* (Fig. 2C) – and *not* their amplitudes – for calculating the angular sensitivity. This is because the modes have different phase constants, and are absorbed along a rhabdom much longer than their beat period. As a result, they appear to be absorbed independently. In this case the resulting angular sensitivity (Fig. 2E, continuous line) is less close to the Airy pattern (broken line).

3.3 *The Role of Higher Order Modes (LP_{11} and LP_{12})*

A complication we have not mentioned up till now, is the fact that if LP_{02} is bound in the cone stalk, two other modes, LP_{11} and LP_{12} are necessarily also bound, because the waveguide parameter (V) of the cone would be large enough. Now there are two possibilities. First, the rhabdom diameter might be so small that only LP_{01} is bound in the rhabdom. This means that LP_{11} and LP_{12} are radiated away when travelling along the tapered cone stalk, mainly absorbed by surrounding pigment cells and not in the rhabdom. With such a small rhabdom diameter LP_{02} will not be bound in the rhabdom, but this does not matter, because all its power has already transferred to LP_{01} during the passage through the cone stalk. The power of LP_{11} or LP_{12} could not be transferred to LP_{01}, because these modes all have different angular symmetries, and can not become coupled in a cylindrically symmetrical structure like the cone (Snyder 1970).

The second possibility is that LP_{11} (or even LP_{12}) is bound in the rhabdom because the rhabdom diameter is large enough. This would broaden the angular sensitivity significantly, as shown in Fig. 3 (see also Land et al. 1987; Nilsson et al. 1987). Figure 3A shows the amplitude of LP_{11}, which is not circularly symmetrical, but instead has two lobes. If LP_{11} is also absorbed in the rhabdom this would result in an angular sensitivity as shown in Fig. 3B: LP_{11} broadens it to almost twice the angular sensitivity of LP_{01}. Here we must add intensities, not amplitudes, because LP_{01} and LP_{11} are absorbed independently (see above). The on-axis sensitivity is not affected by LP_{11}, because the asymmetrical LP_{11} has zero on-axis sensitivity. Interestingly, the broadening may be used for controlling the angular sensitivity (e.g. when dark adapting, Land et al. 1987) because the pupil can effectively control the amount of LP_{11} power absorbed in the rhabdom (Smakman et al. 1984; Nilsson et al. 1987).

3.4 *Predictions from the Mode-Coupling Hypothesis*

3.4.1 Large Fringes. A prediction of the hypothesis that the cone stalk mimics the Airy pattern is that the far field radiation pattern of the ommatidium should show a relatively large fringe (see Fig. 2D) with about 2% of the intensity of the main lobe. This is much larger than the 0.8% expected for the case of the fly. Indeed, this prediction was confirmed, as illustrated in Fig. 4: the far field radiation pattern of a butterfly ommatidium shows a pronounced fringe, with an

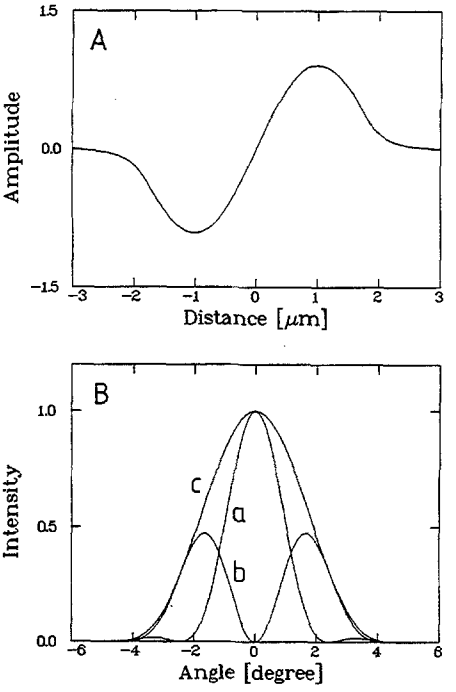

Fig. 3A and B. The role of LP_{11} for the angular sensitivity. **A.** Amplitude of LP_{11} at the distal end of the cone stalk, parameters as in Fig. 2. **B.** Angular sensitivity of LP_{01} and LP_{02} with superimposed amplitudes (*a*), of LP_{11} (*b*), and of LP_{01}, LP_{02}, and LP_{11} together (*c*)

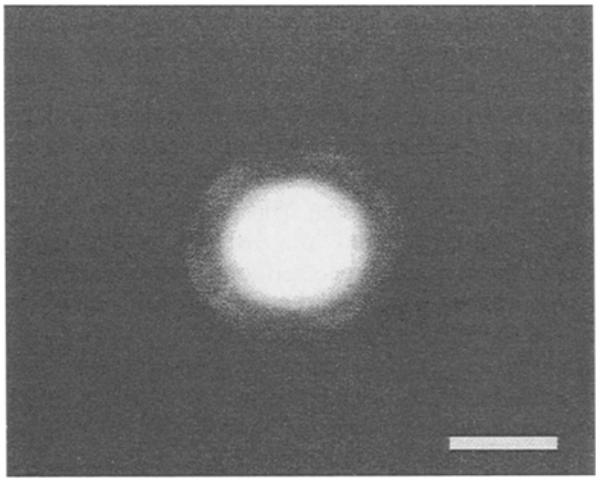

Fig. 4. The output from one facet of *Gonepteryx rhamni* projected at infinity ($\lambda \approx 590$ nm). The fringe around the central lobe is somewhat disturbed by retinal nystagmus. *Scale bar:* 3°

estimated height of about 2% of the peak height. Also at other planes, e.g. in the deep pseudopupil (Nilsson et al. 1987), similar fringes can be observed. In the fly, however, fringes like these were never observed (Van Hateren 1984).

3.4.2 Conspicuous Intensity Patterns. Above we showed that the two modes LP_{01} and LP_{02} together can match the Airy pattern very well. If we illuminate the eye with an on-axis plane wave, the resulting Airy pattern excites these modes in the distal end of the cone stalk; the cone stalk would then convert them to LP_{01}, which travels through the rhabdom, is reflected by the tapetum, and enters the cone stalk from the antidromic direction. If the cone stalk works as a mode convertor, it will do so in both directions: it will split the antidromic LP_{01} into a mixture of LP_{01} and LP_{02} that again mimics the Airy diffraction pattern. As a result the radiation coming back from the cone stalk must look similar to the radiation we can find close to the focus of an ideal lens (Li and Wolf 1984). This prediction was confirmed qualitatively, as shown in Figs. 5 (theory) and 6 (photographs). Figure 5A shows the intensity on the axis of symmetry of a small lens (diameter 20 μm, $F=1.65$, $\lambda=650$ nm). Two remarks: first, the maximum intensity is not at the geometrical focus (Kuiper 1966). The pattern at the focus, however, is the Airy diffraction pattern. Second, there are maxima and minima between focus and lens ($z=0$–40). This is also shown in Fig. 5B, in a plane perpendicular to the axis of symmetry, at three positions indicated in Fig. 5A. Indeed, these local minima and maxima, often only a few micrometers from each other, were observed in the butterfly eye. In Fig. 6h, i two examples are shown, observed through a water-immersion microscope which approximately neutralizes the cornea. Similar patterns are expected around the plane of the lens, and this was also confirmed experimentally (Fig. 6a–e). Patterns like these were never observed in the eye of the fly, which is again evidence for a rather different design of the two eyes. A notable feature of these patterns is that they are not very sensitive to changes in wavelength (Fig. 6f, g). This means that the LP_{01}/LP_{02} pattern and the Airy diffraction pattern behave similarly when the wavelength changes.

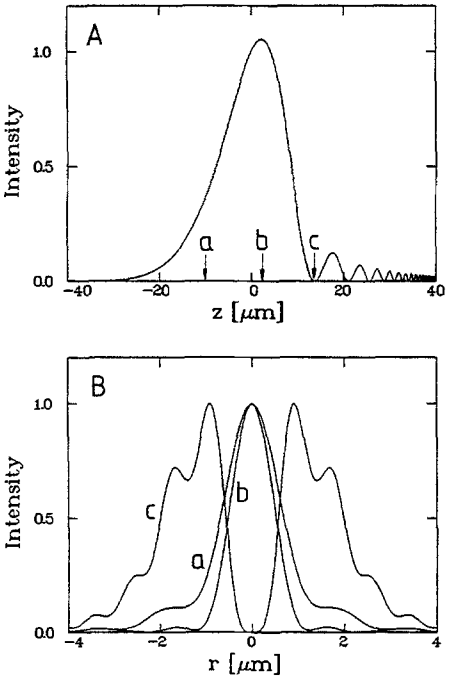

Fig. 5A and B. Intensity patterns around the focal plane of an aberration-free lens. **A.** Intensity on the symmetry axis of the lens as a function of the distance z from the focal place ($z=0$). Positive z: towards the lens. Parameters: lens diameter 20 μm, F-number 1.65, wavelength 650 nm, refractive index behind lens 1.38. **B.** Intensity in three planes perpendicular to the symmetry axis, as a function of the distance r to the symmetry axis; $z=-10$ μm (*a*), $z=2.45$ μm (*b*), $z=13.7$ μm (*c*). For clarity all curves were normalized to 1

3.4.3 Anatomical Correlates. Up till now we have just assumed that the cone stalk functions as a kind of mode convertor, transferring the power present in LP_{02} to LP_{01}. Electron micrographs indicate that there is a good deal of fine structure in the cone stalk (Fig. 7). These structures are, however, much too small to allow any reliable measurements of refractive index. But it is obvious from the electron micrographs that the cone stalk cannot be optically homogeneous: the refractive index in biological material is mainly determined by the protein concentration, and in Fig. 7 mainly proteins are stained. Thus the cone stalk is a tapered waveguide with an inhomogeneous refractive index. Structures like that have been investigated, especially tapered slab waveguides, and have been shown to display strong mode coupling (Lim et al. 1979; Nelson 1975). Therefore, the structure we found in the cone stalk of the butterfly might very well convert LP_{02} to LP_{01}, although we have no direct proof of that.

4 Discussion

We have already stressed that the task a good photoreceptor faces is to mimic the Airy diffraction pattern as well as possible. Another way to look at this is the following. Suppose that a lens projects a diffraction pattern at a certain level, and we want to trap as much power as possible in a waveguide. If we only use LP_{01}, which is approximately gaussian shaped with no sidebands, we will only capture the power in the main lobe of the diffraction pattern, but loose the power in

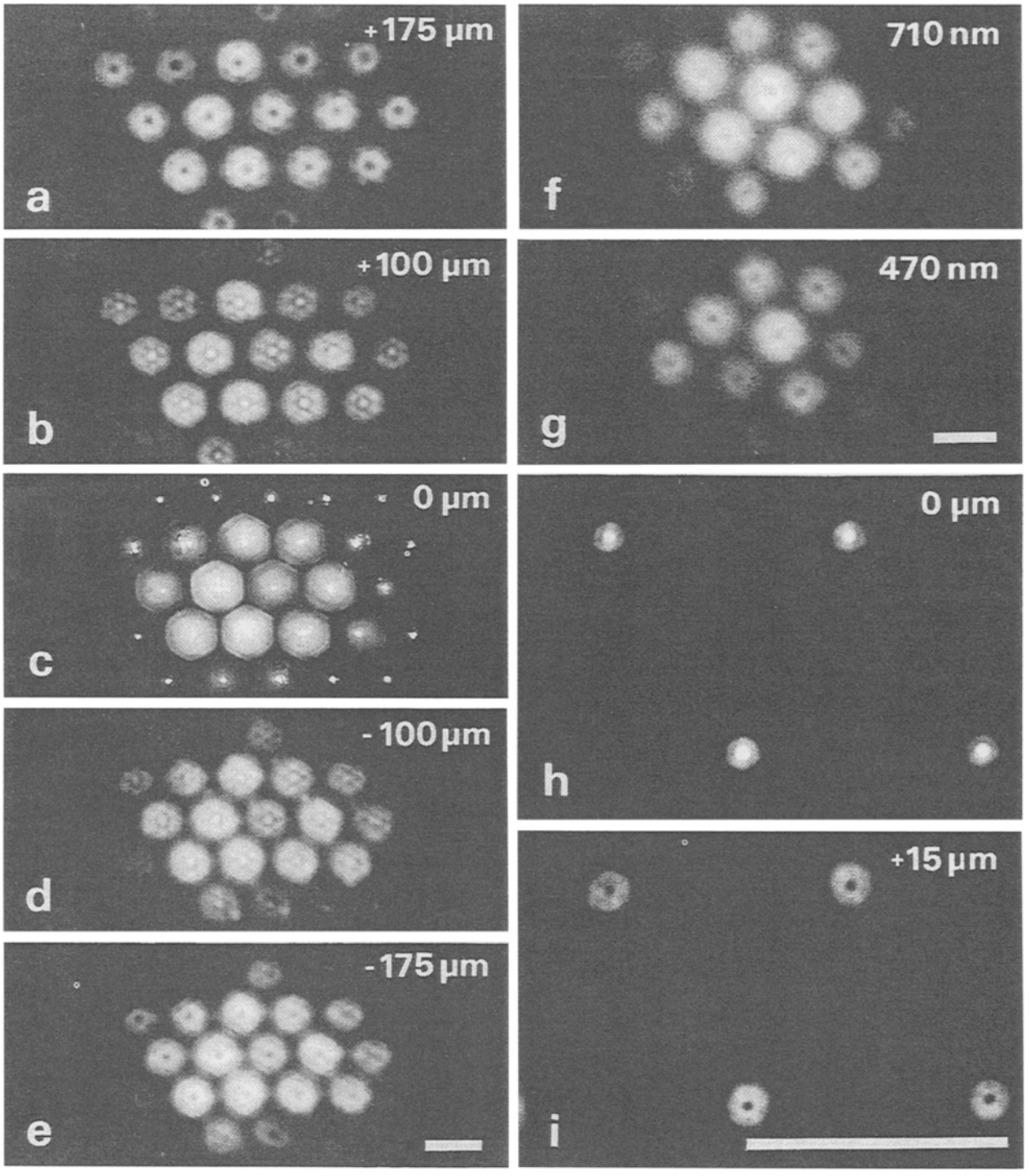

Fig. 6a–i. Photographs of patterns produced by orthodromic illumination of live intact eyes of butterflies. **a–e** shows the distinct interference patterns near the corneal plane in *Clossiana euphrosyne* at $\lambda = 590$ nm. The series is centered around the best focus of the corneal facets (*c*). In **a** and **b** the focus is shifted to 175 and 100 µm outside the corneal plane, which produces the same patterns as when the focus is shifted equally much inside the corneal plane. In **f** and **g** the out of focus pattern (here + 100 µm) in *Aphantopus hyperantus* is observed through an image intensifier. The same features are seen over the entire spectral range of the tapetum (470–710 nm). Observing the eye ♂ of *Lycaena phlaeas* with corneal neutralization (**h** and **i**), demonstrates that the pattern changes rapidly over a very narrow range of depth ($\lambda = 590$ nm). The pattern seen in **h** is probably very close to the back focal plane of the corneal lens. All the above phenomena were observed in the four species investigated (including the Sulfur butterfly *Gonepteryx rhamni*) but *Aphantopus* was preferred for the experiment in **f** and **g** because of the exceptional broad spectral range of the tapetum. *Scale bars:* 20 µm

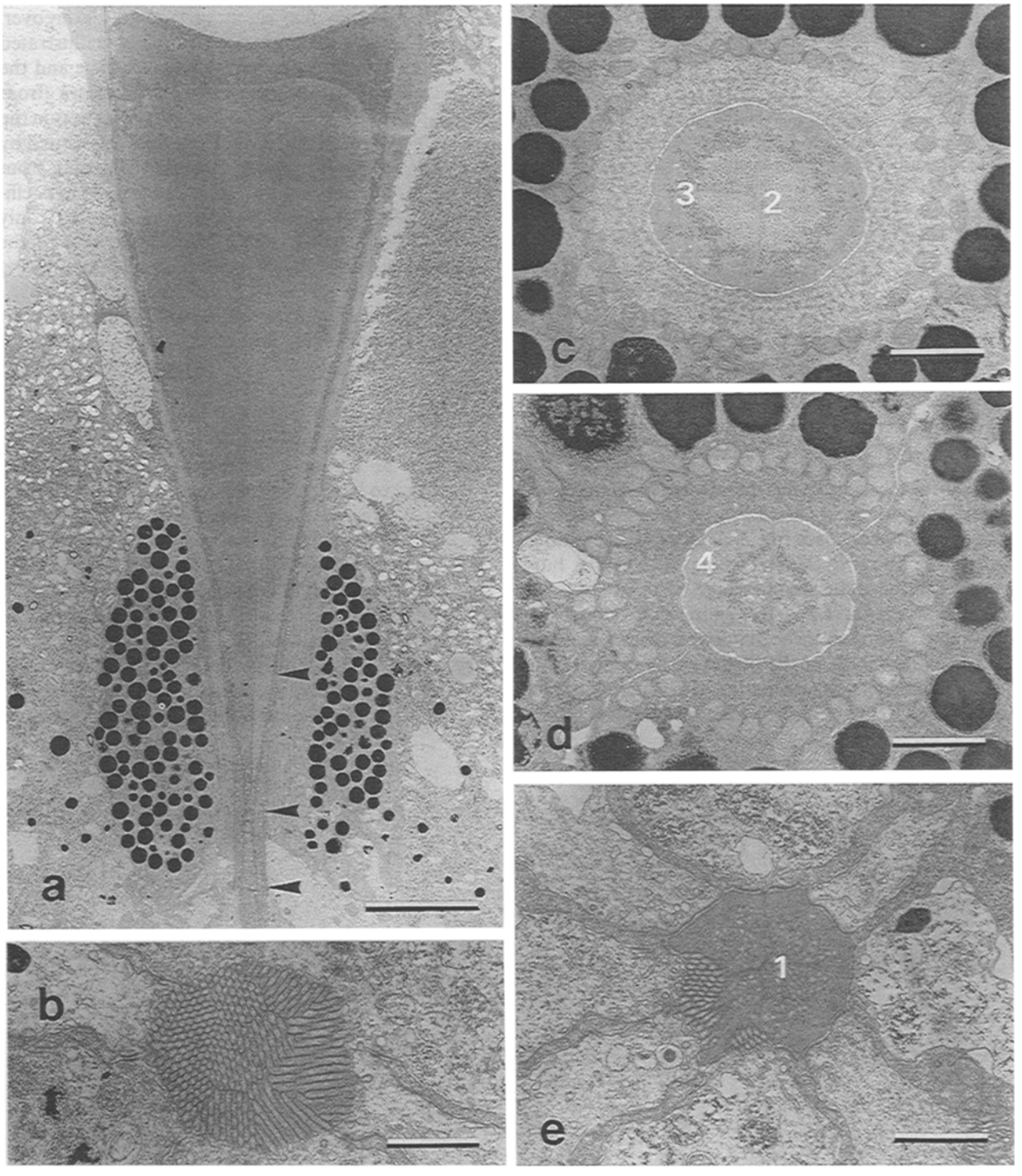

Fig. 7a–e. The ultrastructure of a crystalline cone of *Argynnis paphia*. In **a** an entire cone is seen with the proximal part surrounded by primary pigment cells. The interpretation of the cone stalk as part of the waveguide is supported by the fact that pigment granules never come closer than about 1 μm to the border of the cone stalk. The rhabdom, which is known to act as a waveguide, is seen in cross-section at higher magnification in **b**. The region of interest in this study is marked with *arrows* in **a**, and corresponding cross-sections are shown in **c–e**. Four distinct zones can be distinguished in the cone stalk (representative areas are indicated by the *white numbers 1–4*). The core in the proximal part (*1*) differs in its fine structure from the core more distally (*2*). Especially the distal part of the core is lined with a granular layer (*3*) which in turn is covered with a homogeneous outer layer (*4*). The same structures were found in all other species listed in Methods, although the most favorable fixations were obtained with *Argynnis paphia*. *Scale bars:* **a**, 5 μm; **b–e**, 1 μm

Table 1. Comparison of the power present in the main peak and the first fringes of the Airy diffraction pattern (Born and Wolf 1965, p. 398), the power caught by using increasing numbers of the symmetrical modes (LP_{0i}), and the broadening of the resulting angular sensitivity compared to the Airy pattern. *Main peak* (fly optics): lens diameter $D=20$ μm, F-number of lens $F=2.2$, waveguide radius $b=1$ μm, refractive index of waveguide $n_1=1.38$, refractive index of surrounding media $n_2=1.35$, wavelength $\lambda=650$ nm. *+1st fringe:* $D=20$ μm, $F=1.65$, $b=1.8$ μm, $n_1=1.40$, $n_2=1.35$, $\lambda=650$ *nm. +2nd fringe:* $D=20$ μm, $F=1.65$, $b=1.8$ μm, $n_1=1.40$, $n_2=1.35$, $\lambda=550$ nm

power in:	Airy	On-axis efficiency		halfwidth of acceptance function
main peak	83%	LP_{01}:	79%	+15%
+1st fringe	91%	$LP_{01,02}$:	88%	+ 9%
+2nd fringe	94%	$LP_{01,02,03}$:	90%	+ 7%

the first fringe, because it has the wrong phase. If we are prepared, however, to use LP_{02} as well, which has exactly one sideband (see Fig. 2A), we can also capture much of the power in the first fringe (see Fig. 2B), but now we will loose the second fringe. Using a series of higher order modes (LP_{03}, LP_{04}, etc.) an ever increasing number of fringes can be matched by the increasing number of sidebands of the higher order modes. But the cone diameters and refractive indices required for these modes to be bound in the cone stalk make it unlikely that they play an important role. Moreover, the gain in using them is not very large, as is illustrated in Table 1. There the power in the main lobe and the various fringes in the Airy diffraction pattern (from Born and Wolf 1965) is compared with the power in the bound modes of a cone stalk when these are excited by the Airy diffraction pattern. We see that going from just LP_{01} to $LP_{01}+LP_{02}$ increases the on-axis efficiency from 79% to 88%, whereas adding LP_{03} only increases it further to 90%. The broadening of the angular sensitivity shows the same law of diminishing returns.

A complication that the cone stalk has to deal with is the fact that the diffraction pattern has phase curvature: the fronts of equal phase lie on a spherical surface with the center of the lens as the center of curvature (Goodman 1968, p. 64). This has be corrected for by the cone stalk in order to attain a high efficiency. Both this correction and the mode coupling we assume to happen in the cone stalk call for a design of it that presumably produces the rather intricate phenomena observed in the eye. From the work of Nilsson et al. (1984, 1987) we know that the cone stalk also behaves as an extremely powerful lens that – using a geometrical optics model – turns the ommatidium into an afocal telescope. We believe that there is a connection between the lens-like behavior of the cone stalk and its assumed role as a mode coupling device, but we do not yet understand the mechanism that

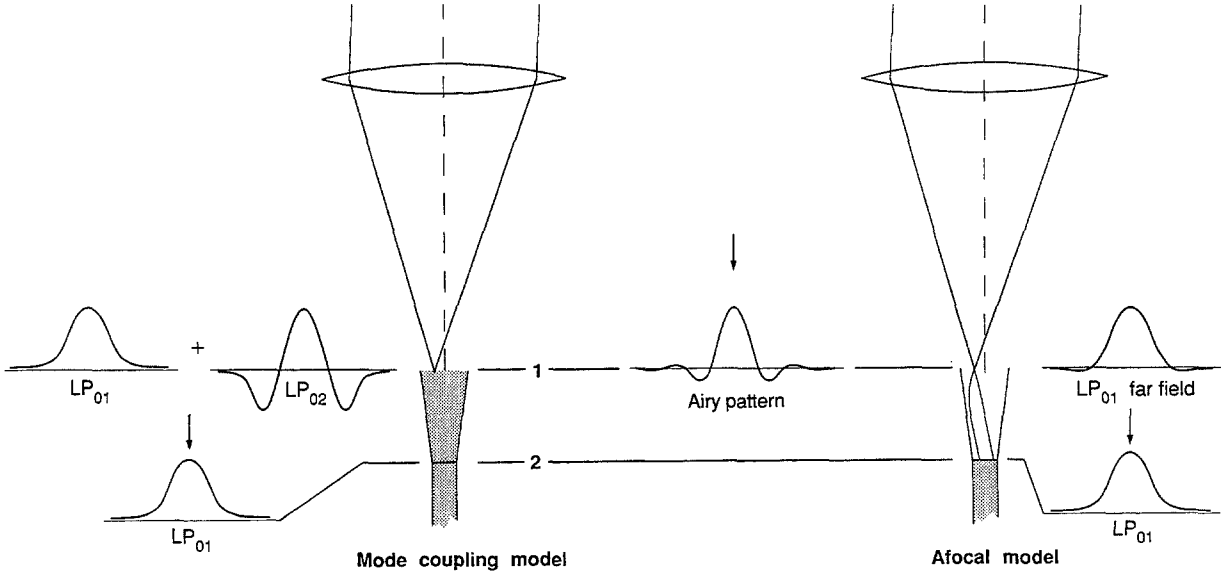

Fig. 8. The two models of the butterfly optical system. Both consist of a corneal lens, cone stalk and rhabdom. Rays are shown for a point source at infinity slightly off axis. In both cases the corneal lens produces an Airy diffraction pattern at level *1*. In our mode-coupling model the Airy diffraction pattern excites a combination of the two modes LP_{01} and LP_{02}, which together mimic the Airy diffraction pattern. When the modes propagate from level *1* to level *2*, the power is transferred entirely to LP_{01} which is supported by the rhabdom. In the afocal model of Nilsson et al. (1987), the cone stalk (between level *1* and *2*) is considered as a second lens instead of as a waveguide. With this interpretation the Airy diffraction pattern would excite the far-field version of LP_{01} which through the cone lens is transformed to the near-field pattern of LP_{01} at the level of the rhabdom tip

unites these two remarkable properties. Indeed, the structure of the cone stalk (Fig. 7) indicates that its optics is far from simple.

The experimental results show that some kind of matching of the Airy pattern must take place, and that the butterfly ommatidium performs better than what is possible with a conventional apposition system like that of the fly. This now provides us with a functional explanation of the existence of the specialized optical system in butterfly eyes, and we can imagine a gradual and continuous evolutionary development from the conventional apposition system to that found in butterflies (Nilsson et al. 1987): the selection pressure would act in favor of an increasing match of the mode pattern to the Airy diffraction pattern.

The mode-coupling model presented here is essentially a focal system which is in contrast to the afocal system proposed by Nilsson et al. (1984, 1987). The two models are not really in conflict, however, since the difference only depends on where we define the waveguide aperture. The two models are summarized and compared in Fig. 8. In our mode-coupling model the waveguide is considered to start at the back focal plane of the corneal lens, where the Airy pattern is projected (plane 1 in Fig. 8). In the afocal model the waveguide is instead considered to start at the rhabdom tip (level 2 in Fig. 8). The structure of the cone stalk does not allow a precise determination of the position of the waveguide aperture, and it is clear that waveguide properties must come into action gradually as the wave-front approaches the rhabdom. Both models presently have shortcomings. The mode-coupling model on the one hand does not explain why butterfly ommatidia behave as an afocal system. The afocal model on the other hand does not perform better than focal apposition optics (Dr. Colin Pask, pers. comm.), whereas measurements (Fig. 1) and evolutionary arguments (Nilsson et al. 1987) suggest butterfly optics do. Moreover, the waveguide properties of the cone stalk must be taken into account (because of its small diameter) even if it is being interpreted as a lens. Nevertheless, we believe that the models will be reconciled, and the apparent shortcomings removed, once a more complete understanding of the optics of the cone stalk is available. Until then, there is no need to reject one of these models in favor of the other. In fact, the understanding of evolution of optical mechanisms is greatly improved (see also Nilsson et al. 1987) because the two models together can bridge the entire gap from conventional apposition to refracting superposition.

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Appendix

Modes and the excitation of modes by an Airy diffraction pattern (Figs. 2 and 3) were calculated as described in Van Hateren (1984). The intensity I of an diffraction pattern near focus (Fig. 5) was calculated as follows (see Li and Wolf 1984):

$$I(r,z)=\left[\frac{2n_0 f}{za^2}\int_0^a \mathrm{d}x x J_0\left(\frac{2\pi n_0 x r}{\lambda z}\right)\times\cos\left(\frac{\pi n_0 x^2}{\lambda}\left(\frac{1}{z}-\frac{1}{n_0 f}\right)\right)\right]^2+\left[\frac{2n_0 f}{za^2}\int_0^a \mathrm{d}x x J_0\left(\frac{2\pi n_0 x r}{\lambda z}\right)\times\sin\left(\frac{\pi n_0 x^2}{\lambda}\left(\frac{1}{z}-\frac{1}{n_0 f}\right)\right)\right]^2,$$

where r is the distance from the axis of symmetry of the lens, z the distance from the back principal plane of the lens, n_0 the refractive index of the medium behind the lens, f the focal distance of the lens (in vacuum), a the radius of the lens, x an integration variable, J_0 a Bessel function of the first kind, and λ the wavelength of the light (in vacuum).

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